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Emergence time in forest bats: the influence of canopy closure

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ABSTRACT

The role of the forest canopy in protecting bats roosting in forest from predators is poorly known. We analysed the effect of canopy closure on emergence time in *Barbastella barbastellus* in a mountainous area of central Italy. We used radio-tracking to locate roosts and filmed evening emergence. Comparisons were made between roosts in open areas and those in dense forest. Median emergence time and illuminance were correlated. Moreover, from pregnancy to late lactation bats emerged progressively earlier, probably because of the exceptionally high wing loading affecting pregnant bats and the high energy demand of lactation. A significant influence of canopy closure on median emergence time was revealed after adjusting for the effects of light and reproductive state. Bats in open habitat emerged later than those roosting beneath closed canopy. In cluttered habitats, predators relying on vision may find it more difficult to detect and catch bats at light levels which would offer more chances of success when attacking prey in open habitats. Bats in dense forest are less vulnerable to predators and may take advantage of an earlier emergence by prolonging foraging. Although more vulnerable, lactating females roosting at open sites may benefit from warmer roosting conditions. Roosts in dense forest may be preferred under intense predation pressure. Forest management should favour canopy heterogeneity to provide bats with a range of roosting conditions. Our work emphasises the role of a fine-grained spatial scale in the roosting ecology of forest bats.

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1. Introduction

Forest represents a major habitat for bats (Barclay and Brigham, 1996). Several bat species select it for either foraging (Entwistle et al., 1996; Humes et al., 1999; Jung et al., 1999;

Kerth et al., 2001a; Bontadina et al., 2002) or roosting for at least part of their annual life cycle (for review see Kunz and Lumsden, 2003). Consequently, forest structure and management may critically influence availability of suitable habitat (Entwistle et al., 1996; Patriquin and Barclay, 2003).

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Canopy structure may play an important role in providing the spatial complexity forest bats require. Nonetheless, little attention has been paid to its influence on bat species assemblages (Wunder and Carey, 1996). A better understanding of the significance of canopy structure for bat conservation ecology is needed to avoid negative impacts caused by incorrect forest management.

On leaving the roost to go feeding in the evening, bats exhibit patterns of timing and aggregation whose causes have been addressed by several studies (e.g. Jones and Rydell, 1994; Speakman et al., 1995, 1999; Shiel and Fairley, 1999; Duvergé et al., 2000). However, given the logistic difficulties posed by studies on tree-roosting bats, most work published on this topic is biased towards species roosting in caves or buildings. Although miniaturisation of transmitters employed for radio-tracking has considerably increased the number of studies on tree-roosting bats (e.g. Lacki and Schwierjohann, 2001; Law and Anderson, 2000; Lumsden et al., 2002; Sedgeley and O'Donnell, 1999a,b; Sedgeley, 2001; Russo et al., 2004, 2005; Willis and Brigham, 2004), emergence behaviour in these species remains little investigated (but see e.g. Jones, 1995).

The onset of emergence behaviour is basically controlled by the endogenous rhythm synchronised with the external 24-h light–dark cycle (Erkert, 1982). However, bats may adjust emergence timing according to several other factors, whether exogenous (i.e. environmental) or endogenous (i.e. related to life cycle phases). Among the former, local levels of light intensity, such as those determined by clouds, or canopy cover, may cause variation in emergence time (Howard, 1995; Shiel and Fairley, 1999). Likewise, rain has been found to disrupt, or inhibit, emergence behaviour (Entwistle et al., 1996; Shiel and Fairley, 1999). During the reproductive season, some species have been found to emerge progressively earlier from pregnancy to late lactation (Shiel and Fairley, 1999; Duvergé et al., 2000). To cope with the high energy requirements posed by raising their young, lactating females emerge earlier to prolong foraging time and ensure access to crepuscular insect prey. On the other hand, pregnant bats exhibit decreased flight performances due to their exceptionally high wing loading, which renders them more vulnerable to predatory birds. Consequently, such females tend to emerge progressively later as pregnancy advances (Duvergé et al., 2000).

Although the debate is still open (Speakman et al., 2000), predation by birds relying on vision for hunting appears the most probable selective force for the evolution of nocturnality in bats (Fenton et al., 1994; Rydell and Speakman, 1995; Speakman, 2001). In general, predation has been recognised as a major factor influencing emergence timing and patterns. Non-random, clustered emergence patterns have been interpreted as an anti-predatory strategy (Speakman et al., 1995, 1999; but see Irwin and Speakman, 2003). As with nocturnality, the main predators responsible for such effects would be diurnal birds of prey. Because owls mainly rely on hearing for foraging (e.g. Taylor, 1994), the effect of light on their predation success, and consequently their role in influencing bat emergence behaviour are probably negligible. Emergence time is then taken to be a compromise between the need to start foraging at high light levels, i.e. when most prey is available, and the increased risk of predation faced under such circumstances (Speakman, 1991; Jones and Rydell, 1994).

Bats in roosts close to woodland or hedgerows exhibit an earlier emergence than those roosting in more exposed conditions (Jones et al., 1995; Entwistle et al., 1996; Duvergé et al., 2000). Vegetation cover may reduce the risk of emerging in lit conditions by sheltering bats from predators. For example, *Rhinolophus hipposideros* emerged later at an exposed roost exit than at another located ca 20 m from a tree line (Duvergé et al., 2000). Likewise, *Plecotus auritus* emerged significantly earlier from roosts located at ca 50–100 m from the nearest woodland than from those found at greater distances (Entwistle et al., 1996).

To the best of our knowledge, analogous patterns are not documented for tree-roosting bats. In the latter, variation in emergence time might depend on a finer-grained spatial scale, corresponding to the distance between roosts and neighbouring trees. In other words, even subtle differences in forest structure and density – i.e. in the degree of canopy closure – might result in differential exposure of emerging bats to potential predators.

In our study, we hypothesised that bats are programmed into emerging later in open forest because over time evolution has selected for this. In fact, bats flying later will have experienced less predation from aerial predators. At a certain light intensity, a predator relying upon vision might find catching bats more difficult in a structurally complex environment such as closed canopy compared with open sites. Both prey detection and manoeuvrability may be impaired. Consequently, being better protected, bats in dense forest could emerge earlier than those in areas where trees are more spaced out. This behaviour may be hard-wired even where predators are rare.

2. Materials and methods

2.1. Model species

We chose the barbastelle bat (*Barbastella barbastellus*) as a model species to explore our hypothesis. *B. barbastellus* is rare in Europe (Urbańczyk, 1999), classified as “Vulnerable” globally (Hutson et al., 2001) and “Endangered” in Italy (Bulgarini et al., 1998). The population we examined mainly selects roosts in spaces behind loose bark on dead beech trees (Russo et al., 2004). Roost trees are mostly found in unmanaged forest areas; roosts are more often south-facing and at greater heights above ground than random cavities. Both sexes switch roosts often, probably to maintain or increase knowledge of alternative roosts (Russo et al., 2005).

2.2. Study area

Observations were carried out during July and August in 2003 and 2004 in a 700-ha mountainous area of the Abruzzo, Lazio and Molise National Park (41°48' N, 13°46' E), central Italy, where mean elevation is ca 1500 m a.s.l. (range 1278–1924 m a.s.l.). In our study area *B. barbastellus* roosts exclusively in trees (Russo et al., 2004, 2005). The substrate is mainly limestone, and extensively covered with beech (*Fagus sylvatica*) forest. Another habitat occurring in the area is pasture, mostly scattered with trees. In most of the area no logging has

occurred since 1956; limited selective logging does take place occasionally in some forest stands (Russo et al., 2004).

2.3. Location of roosts

All roosts were located by radio-tracking. Bats were captured with 2.5×6 m and 2.5×12 m mist-nets (50 denier, 38 mm mesh) placed near cattle troughs. We erected nets soon after dusk and kept them in place for 2–4 h. Body mass and forearm length of captured subjects were recorded to the nearest 0.1 g and 0.1 mm, respectively. Wings were trans-illuminated to distinguish juveniles from adults, the former showing cartilage epiphyseal plates in finger bones and more tapered finger joints (Anthony, 1988).

Pregnancy was ascertained by palpation (Racey, 1988), and lactation by the presence of enlarged nipples bordered by a hairless skin area and by extruding milk with gentle finger pressure on the nipple base. Females tagged between 4 and 12 July, categorised as “pre-lactating”, showed no sign of lactation: they included obviously pregnant females as well as bats with no evident signs of pregnancy (probably early pregnant subjects). Females tagged between 11 July and 2 August were clearly lactating. Some of those tagged between 6 and 19 August were lactating, but not others: we categorised them as bats in “late lactation – postlactation”. Males were rarely captured in the study area.

Bats were fitted with 0.48 g LB-2 Holohil (Carp, Canada) radio-tags glued between the shoulder blades with Skinbond® after partly trimming the fur. Captures were carried out under licence from the Park authorities.

During the daytime we tracked radio-tagged bats on foot, using an Australis 26 K radio-receiver (Titley Electronics Pty Ltd., Ballina, NSW, Australia) and a three-element hand-held directional antenna. Roost tree position was assessed with

a Global Positioning System receiver and noted on a 1:25,000 map (Istituto Geografico Militare, Florence).

2.4. Data collection

We chose a number of focal subjects per radio-tracking session and filmed evening emergence with a Night-Shot function Sony PC 115 digital video-camera. From all trees, we assessed visually the percent degree of canopy closure from the base of the tree (Russo et al., 2004). From sunset until the end of emergence, ambient temperature was measured every minute with a digital thermometer to the nearest 0.1 °C, and in most cases illuminance (in lux) at ground level with a Delta Ohm photo-radiometer (spectral range 450–760 nm, operational range 0–200,000 lux, resolution ≤ 200 lux = 0.1; > 200 lux = 1). To represent as much as possible the level of light available at the roost tree site, light was measured by pointing the sensor towards the open sky for roost trees in openings, otherwise towards canopy for trees in dense forest. We also estimated wind speed according to the Beaufort scale and cloudiness on a 0–8 scale. Work was not carried out on rainy evenings.

To avoid pseudo-replicating the observations, only one video tape per roost was used for analysis. Recordings whose quality did not allow accurate measurement of emergence timing were discarded.

In all, we selected 19 roost trees used by female groups: 11 – categorised as “loose canopy structure” trees – were in small forest openings (canopy closure = 0%, distance from closest neighbouring tree < 15 m), eight – “dense canopy structure” trees – in dense forest patches (mean canopy closure \pm SD = $55.6 \pm 20.3\%$, range 25–75% – Fig. 1). The videos were then reviewed in the laboratory. Some video sequences shot in August showed a bimodal emergence pattern. Following



Fig. 1 – Typical examples of *Barbastella barbastellus* roost trees considered for this study. Roost tree in A: forest opening; and B: dense forest.

Duverg  et al. (2000), we analysed only the first peak, corresponding to bats believed to be adults. Those emerging later often exited the roost after exhibiting peculiar behaviours such as wing stretching. Such bats were probably volant juveniles (Russo et al., 2005).

For each emergence event, we assessed group size and recorded the time each bat emerged to the nearest minute. For analysis, we used the time the median bat left the roost and related it to sunset time (Duverg  et al., 2000) as provided by the GPS receiver for the corresponding observation day and location.

2.5. Experimental design and statistical analysis

Selected observations were sorted by date (day and month, independent of year) and each was labelled with the number of days from the first observation (day 1 corresponding to the earliest date). The resulting variable is hereafter called “day of observation”.

In preliminary data exploration, correlation analysis was used to detect factors which may influence emergence time. Of the environmental parameters measured, wind speed, ambient temperature and cloudiness had no effect on emergence ($P > 0.05$). The remaining variables – day of observation and illuminance – were entered as covariates in General Linear Model ANCOVAs (Analysis of Covariance) with canopy structure (loose or dense) used as the main effect. Resulting adjusted means represented only the canopy structure effect, independent of the covariates. The variable “day of observation” accounted for possible shifts in emergence time due to female reproductive stage, as noticed in other species (Shiel and Fairley, 1999). Apart from the hypothetical anti-predatory benefits under investigation, the degree of canopy closure is likely to have influenced light levels, and in turn emergence time. In fact, it may be hypothesised that light level controls emergence time, i.e. bats might emerge later in open habitats, but at the same ambient light level at which bats emerge in closed habitats.

We used illuminance as a covariate in the ANCOVA to disentangle such potentially confusing effects. If, after adjusting for light levels and reproductive period, bats in open habitats are found to emerge later, then this difference may best be explained in terms of different habitat structure. The hyperbolic extinction pattern of illuminance around sunset time was made linear by a log transformation. Normality of residuals was checked with a Ryan-Joiner test. Significance was set at $P < 0.05$. All tests were performed with MINITAB for Windows release 13.32.

3. Results

On average, the median bat emerged 19.5 ± 6.6 min after sunset (range 5–31 min, $N = 19$). Group size averaged 12.4 ± 5.0 (range 3–25). Group size did not correlate significantly with emergence time ($r_s = -0.37$, $N = 19$, n.s.).

Day of observation clearly influenced emergence time. From pregnancy to late lactation, females emerged progressively earlier (Fig. 2). Day of observation also correlated positively with illuminance ($N = 15$, $r_s = 0.68$, $P < 0.01$), mainly

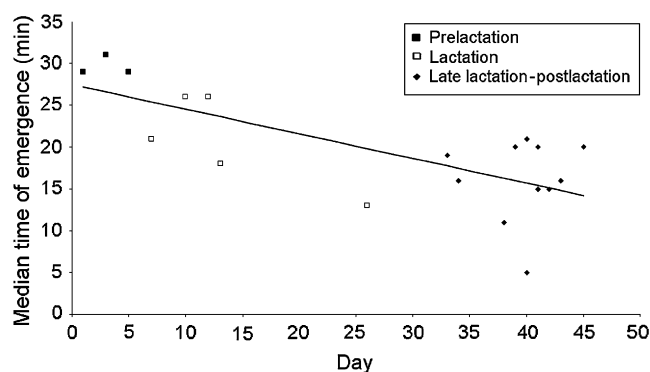


Fig. 2 – Regression line of emergence time of median bat plotted vs. day of observation (day 1 = 5 July 2004; day 45 = 19 August 2004; $N = 19$). Equation was (median time of emergence = $27.202 - 0.295$ day); $R^2(\text{adj}) = 49.1\%$, $P = 0.001$.

reflecting the fact that illumination was higher at earlier emergence times (i.e. when bats later on in the reproductive season left the roosts). Illumination and median emergence time were negatively correlated ($r_s = -0.58$, $N = 15$, $P < 0.05$; Fig. 3): this was simply the consequence of later emergence events occurring at lower ambient light levels and vice versa. The interaction between canopy closure and ambient light may be noticed from a visual inspection of the scatterplot in Fig. 3. Emergence events recorded, respectively, at closed and open sites at similar illuminance levels differed in time, and tended to occur earlier at closed sites.

An ANCOVA carried out on all female groups using day of observation as a covariate showed that both day of observation and canopy structure had a significant effect, adjusted means being 22.6 ± 1.1 min and 17.6 ± 1.3 min in loose and dense canopy structures, respectively (Table 1). A further ANCOVA, with both day of observation and log (illuminance) entered as covariates, was carried out for 15 roosts (Table 1). After adjusting for significant effects of both covariates,

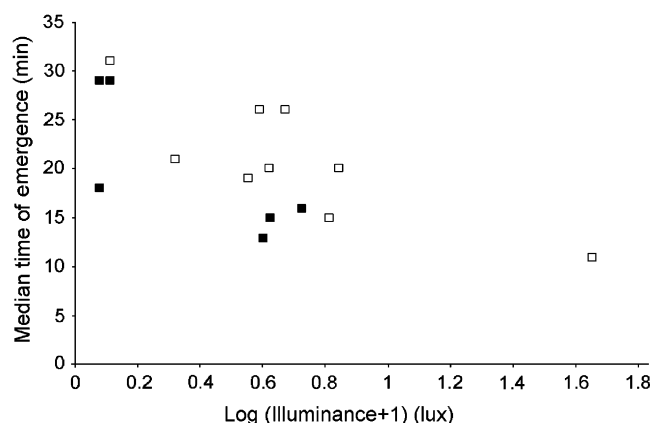


Fig. 3 – Scatterplot illustrating the relationship between illuminance values – transformed as log (illuminance + 1) – and emergence time of median bat ($r_s = -0.58$, $N = 15$, $P < 0.05$). Open squares: open canopy sites; filled squares: closed canopy sites.

Table 1 – Analysis of covariance (General Linear Model) on median emergence time in female *Barbastella barbastellus* groups

Source of variation	d.f.	Adj. MS	F	P
(A)				
Day of observation (covariate)	1	537.57	36.65	<0.001
Canopy structure	1	147.65	10.07	0.006
Error	16	14.67		
Total	18			
(B)				
Day of observation (covariate)	1	87.89	8.71	0.001
Log (illuminance) (covariate)	1	57.70	5.72	0.04
Canopy structure	1	92.62	9.18	0.01
Error	11	10.09		
Total	14			

Canopy structure (loose–dense) was entered as main effect. (A): N = 19, day of observation was used as a covariate. (B): N = 15, both day of observation and log (illuminance) were used as covariates. Days of observation numbered from day 1 (July 5, 2004) to day 45 (August 19, 2004); illuminance was expressed in lux; d.f. = degrees of freedom; Adj. MS = adjusted mean squares.

canopy structure revealed the same pattern, emergence being delayed in open situations relative to closed canopy (adjusted means 22.9 ± 1.1 min and 17.2 ± 1.4 min in loose and dense canopy structures, respectively).

4. Discussion

4.1. Emergence behaviour in *Barbastella barbastellus*

Evening emergence time in echolocating bats has been found to relate to both flight speed and diet in a cross-species comparison (Jones and Rydell, 1994). Species characterised by a slow flight (corresponding to low wing loading) tend to emerge later to compensate for the potentially higher predation rate they face, and vice versa. On the basis of the mean emergence time value we recorded and assuming a wing loading of 9.1 N/m^2 (see Jones, 1993 for an individual *B. barbastellus*), the species we examined appears to conform to this model. Among European bats, species whose wing loading falls between 9.0 and 10.2 (e.g. *Myotis bechsteinii*, *Eptesicus nilssonii*, *Vespertilio murinus* and *Rhinolophus ferrumequinum*) exhibit similar emergence times (i.e. 25–35 min; Jones and Rydell, 1994).

Moreover, *B. barbastellus* emergence time also corresponds closely to the mean value reported for the temperate zone bats that mainly feed on moths (Jones and Rydell, 1994). The relatively late emergence of *B. barbastellus* is a consequence of the fact that the species' diet mostly consists of moths (Rydell et al., 1996a; Sierro and Arlettaz, 1997), i.e. it does not depend upon crepuscular insects (Rydell et al., 1996b). Thus emergence time appears to be mainly a function of both predation risk and diet specialisation.

When illuminance alone was considered for correlation analysis, the main trend detected was that later emergence times corresponded to lower illuminance (i.e. as expected, bats leaving the roost later did so at lower ambient light levels) and vice versa, resulting in a negative correlation between the

two variables. This trend was evident because of the presence in the sample of emergence events occurring at markedly different times, i.e. at different illumination levels. The positive correlation found between day of observation and illumination suggests that reproductive period was a main component influencing the negative trend found between emergence times and light values. In fact, as shown by our study, *B. barbastellus* also makes emergence time adjustments according to reproductive condition. The tendency of lactating bats to emerge progressively earlier during the reproductive season is in agreement with studies on other species (e.g. Duvergé et al., 2000; Shiel and Fairley, 1999) and confirms that in this period bats face strong energy requirements. The earlier emergence in lactating females suggests that this option still confers some benefits even to moth specialists (i.e. whose preferred prey is still largely available later in the night; Rydell et al., 1996b), probably associated with longer foraging time.

Because the above correlation analyses examined each factor at a time, uncontrolled influences by the other variables inevitably affected the results. After removing the effects of potentially confusing environmental (illuminance) and endogenous (phase of reproductive season) factors with an ANCOVA, median emergence time in *B. barbastellus* was significantly influenced by canopy cover. This is the first account of the effect of canopy cover on emergence behaviour in forest-roosting bats. The earlier emergence noticed beneath closed canopy is most consistent with the explanation that bats in dense forest are less vulnerable to predators, and vice versa. Over time, bats emerging earlier at open sites may have faced strong predation risks, this resulting in the evolution of the anti-predatory strategy highlighted by our analysis.

Caution is advisable in interpreting the outcome of correlative analyses such as those here presented. Many endogenous or environmental factors, often difficult to control and/or test for, may be responsible for patterns of roost selection, roost switching and emergence timing. Therefore, selection pressure exerted by predators might not be the only (or the main) factor responsible for the emergence timing patterns observed. However, our approach still represents a solid one to the issue with respect to others. In fact, direct observation of predation events is rare and quantitative analyses are generally feasible only at sites where exceptionally large colonies congregate (Lee and Kuo, 2001). On the other hand, positioning stuffed predator specimens or broadcasting predator calls in the proximity of roosts to test for bat reaction (Petrzelkova and Zukal, 2001) is unlikely to provide realistic predatory signals and results may be flawed by habituation. Such experiments also often involve owls, which hunt primarily by listening for auditory cues, and may not reflect potentially stronger selective pressures imposed by visually hunting birds of prey. Although predation by owls is unlikely to have acted as a strong evolutionary pressure shaping bat emergence behaviour, it may become locally significant, and these birds' high visual acuity (e.g. Martin, 1977) besides hearing may probably help detect emerging bats especially at open sites. On the other hand, leaving roosts at cluttered sites may limit the risk of being preyed upon by such predators whose manoeuvrability is often reduced in clutter.

Habitat-specific variations in moth (main prey of *B. barbastellus*) circadian activity cannot account for the observed

habitat-specific emergence times. The earlier emergence observed in dense forest might in theory represent a response to an earlier prey availability peak in this habitat. However, given the generally short distance between open and closed sites, bats in open forest would emerge earlier than those in dense forest to reach the closed canopy sites in time to exploit the prey abundance peak. This emergence pattern would be opposite to that we recorded.

B. barbastellus roosting in dense forest patches generally emerged by dropping down through an unobstructed flight distance and commuted beneath the canopy. Those roosting in open situations often moved towards the closest neighbouring forest patch (pers. obs.). In our study area, at least the first activity bout may have been taken place beneath the canopy, i.e. in a situation safer from predators. *B. barbastellus* exhibits considerable plasticity in echolocation calls. In cluttered habitats, calls are effective in providing an accurate description of background (Denzinger et al., 2001), i.e. they may be useful for orientation and prey detection in structurally complex situations such as those encountered beneath the canopy.

Greenaway (2001) noticed that *B. barbastellus* increases foraging time by hunting in the dark areas beneath the canopy. Although no statistical support was presented, the same study reported that roosts found in shaded areas would allow bats to perform up to 2 h of extra flight per night. Although *B. barbastellus* mostly forages above forest canopy (Sierro, 1999), a variety of other habitats is also used, including riparian areas, meadows, hedgerows and forest edges (Denzinger et al., 2001; Greenaway, 2001).

Our study confirms that besides microclimate requirements (Kerth et al., 2001b), defence against predators may play a major role in roost choice. In several bat species, selection of roost cavity features has been thought to be influenced by predation risk (e.g. Ruczyński and Bogdanowicz, 2005). Tree cavity-roosting bats may select roosts whose entrance is only just larger than the bat size, presumably to exclude predators (e.g. Tidemann and Flavel, 1987; Campbell et al., 2005).

In our study area, roost cavities were selected at greater heights than the average available cavities (Russo et al., 2004). This feature, as well as the preference shown for roost entrances facing southern directions, was primarily interpreted as a response to reproducing females' needs for warm conditions for pregnancy and lactation. Selecting a warmer roost may effectively reduce the costs of homeothermy (Kerth et al., 2001b). Roosting high up may also reduce the risk represented by climbing terrestrial predators such as pine martens (*Martes martes*) for roosting bats. However, it obviously does not protect emerging bats from aerial predators.

Although closed canopy probably offers an anti-predatory advantage to emerging bats (this study), it will also inevitably shade roost cavities, leading to cooler roost temperatures. Roosts in open areas, although more exposed to predators, may reduce female thermoregulatory costs during reproduction, whereas the opposite holds for those beneath closed canopy. Although bats in the latter situation may emerge earlier, prolonging foraging time (Greenaway, 2001), this advantage may not compensate for the extra costs of sub-optimal thermal conditions. Therefore the choice of roost type

appears to involve a trade-off between energetic and safety requirements.

4.2. Roost selection and canopy structure

In the same area dealt with in this paper, Russo et al. (2004) found that canopy closure did not score significantly in logistic models of roost tree selection by *B. barbastellus*, which instead relied upon tree condition (dead trees being preferred) and height (tall trees being selected). The emergence timing flexibility we observed may allow *B. barbastellus* to select roost trees characterised by different degrees of canopy closure, i.e. a larger number of roosts providing different microclimates. However, selection for closed canopy might be favoured in the presence of frequent predation events. *B. barbastellus* switch roosts very frequently: in our study area, we observed a roost switch rate of 0.2–0.7 trees/day, mainly depending on female reproductive condition (Russo et al., 2005). Roost switching was most consistent with the hypothesis that the behaviour evolved as a response to converging selective pressures typical of roosting in ephemeral conditions such as those found in forests, including roost lability and predation (Russo et al., 2005). Roost switching would help maintain knowledge of alternate roosts, allowing the bats to move to another roost if the one they are using becomes unsuitable (see also Kurta et al., 2002). In the “predation scenario” hypothesised for roost switching, a roost may become unsuitable if, for instance, it is detected by predators, or if its structure appears too exposed following a sudden increase in predation frequency. In such cases, bats might find it convenient to move from a roost tree in the open, perhaps characterised by an optimal microclimate for lactating females, to another beneath closed canopy, whose sub-optimal thermal conditions may be compensated by better protection from predators.

A further point emphasised by this study is the spatial scale at which structural changes may prove important to roosting bats. Although trees in open habitat were all just a few metres away from cover, this condition did delay emergence. This situation would have been regarded as “protected” in studies focusing on bats using roosts other than trees (e.g. Duvergé et al., 2000). Although difficult to test, even subtle variation in canopy closure is likely to have implications for predation risk and emergence behaviour. Clearly, forest environments pose different adaptive challenges to bats and deserve specific consideration in research on bat ecology and evolution.

5. Conclusions

Although *B. barbastellus* prefers unmanaged forest, it may persist in stands where low management intensity and selective logging are applied, as far as large numbers of dead trees are retained (Russo et al., 2004). Forest succession dynamics should also be considered for long-term conservation of tree-dwelling bats (Jung et al., 2004; Carter and Feldhamer, 2005). In *B. barbastellus* roosting areas, old trees need to be saved too, so that they will replace the dead ones which

fall as a result of mechanical and biological actions (Russo et al., 2005).

Our study suggests that even just within the lactation period – i.e. when, according to expected thermal requirements, roosts most exposed to sun should be preferred – bats may in fact need a range of roosts with different degrees of exposure: some favouring high irradiation, others better sheltered against predators or, possibly, other sources of disturbance (e.g. human presence; Russo et al., 2004).

B. barbastellus avoids roosting in areas of wooded pasture, characterised by a homogeneously loose canopy cover (Russo et al., 2004). Although this observation might simply reflect a correspondingly lower roost tree density, we believe the homogeneously loose canopy cover may be an important factor determining avoidance of this forest structure.

Structural heterogeneity, partly granted by a dense holly understorey, constitutes an important feature in British beech woodlands used by *B. barbastellus*, providing a mixture of roost sites and cover resulting in a wide range of micro-climatic conditions. These best fit the different thermal requirements faced by roosting bats all year round (Greenaway, 2001).

Preserving canopy heterogeneity in forest areas inhabited by *B. barbastellus* appears to be another management aspect to be taken into account. Although small openings around a number of roost trees in a roosting area are acceptable and probably favour thermoregulation by reproductive females, logging should avoid generating large-scale gaps in forest canopy, i.e. excessively large, homogeneous clearings. In mature stands, selection harvest is the only practice capable of maintaining an uneven-aged forest, providing a range of canopy closure conditions at different roost sites. In younger stands, management should encourage the development of canopy heterogeneity during forest growth by favouring the presence of different vertical levels, including dominant, co-dominant, and intermediate trees.

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